

THE RELATIONSHIPS AND EVOLUTION OF THE SOUTHWEST PACIFIC WARBLER GENERA *VITIA* AND *PSAMATHIA* (SYLVIINAE)

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The genera *Vitia* and *Psamathia* include three species of sylviine warblers of forest undergrowth from Micronesia and Melanesia: the Fiji Warbler (*V. ruficapilla*) with races on Viti Levu (*V. r. badiceps*), Vanua Levu (*V. r. castaneoptera*), Taveuni (*V. r. funebris*), and Kadavu (*V. r. ruficapilla*); the Shade Warbler (*V. parens*), a little-known bird of the mountains of San Cristobal, and probably Bougainville (Hadden 1981), in the Solomon Islands; and the Palau Bush-Warbler (*Psamathia annae*), restricted to Palau (Mayr 1945). Baker (1951:221) suggested, on the basis of external morphology, that *P. annae* was allied to *Cettia diphone seebohmi* of Luzon. Pratt et al. (1980) included the Palau bird in *Cettia*, and E. Mayr (in litt.) agrees with this treatment. The position of *Vitia* has been more obscure, although Delacour (1942-43) suggested that it, too, was allied to *Cettia*. Ramsay (1875), in his description of *Vitia*, compared *V. ruficapilla* to *Malurus* (Malurinae) and *Sericornis* (Acanthizinae). Finsch (1876) placed *V. r.* ("Drymochaera") *badiceps* between *Camaropectera* and *Orthotomus* (Sylviinae). Mayr (1936) compared *V. parens* to *Sericornis nouhuysi*, but concluded that the two were not related. Morony et al. (1975) list *Psamathia* after *Cettia*, but place *Vitia* near the end of the Sylviinae with other genera of obscure affinity such as *Ortygocichla* and *Megalurulus*. This paper presents evidence that *Vitia* and *Psamathia* are Pacific island representatives of *Cettia*, closely related to *C. diphone*.

METHODS

The authors independently made observations and tape recordings of *V. r. badiceps* on Viti Levu (Orenstein, June 1974; Pratt, July 1977). Pratt also observed *V. r. castaneoptera* on Vanua Levu, but his tape recordings of it were lost. Pratt made extensive observations and recordings of *Psamathia annae* during several visits to Palau (Pratt et al. 1980) and observed an introduced population of the Japanese Bush Warbler (*Cettia diphone cantans*) on Oahu in the Hawaiian Islands intermittently from 1974-1980. Both authors studied tape recordings of various *Cettia* species in the collection of the Laboratory of Ornithology, Cornell University. Our own recordings are now archived in that collection. Orenstein examined study skins of *Cettia*, *Vitia*, and *Psamathia* in the American Museum of Natural History and the Museum of Zoology, University of Michigan.

CHARACTER ANALYSIS

Song.—The song of *V. r. badiceps* is a clear unmodulated whistle, usually interrupted by brief pauses near the beginning, rising gradually in

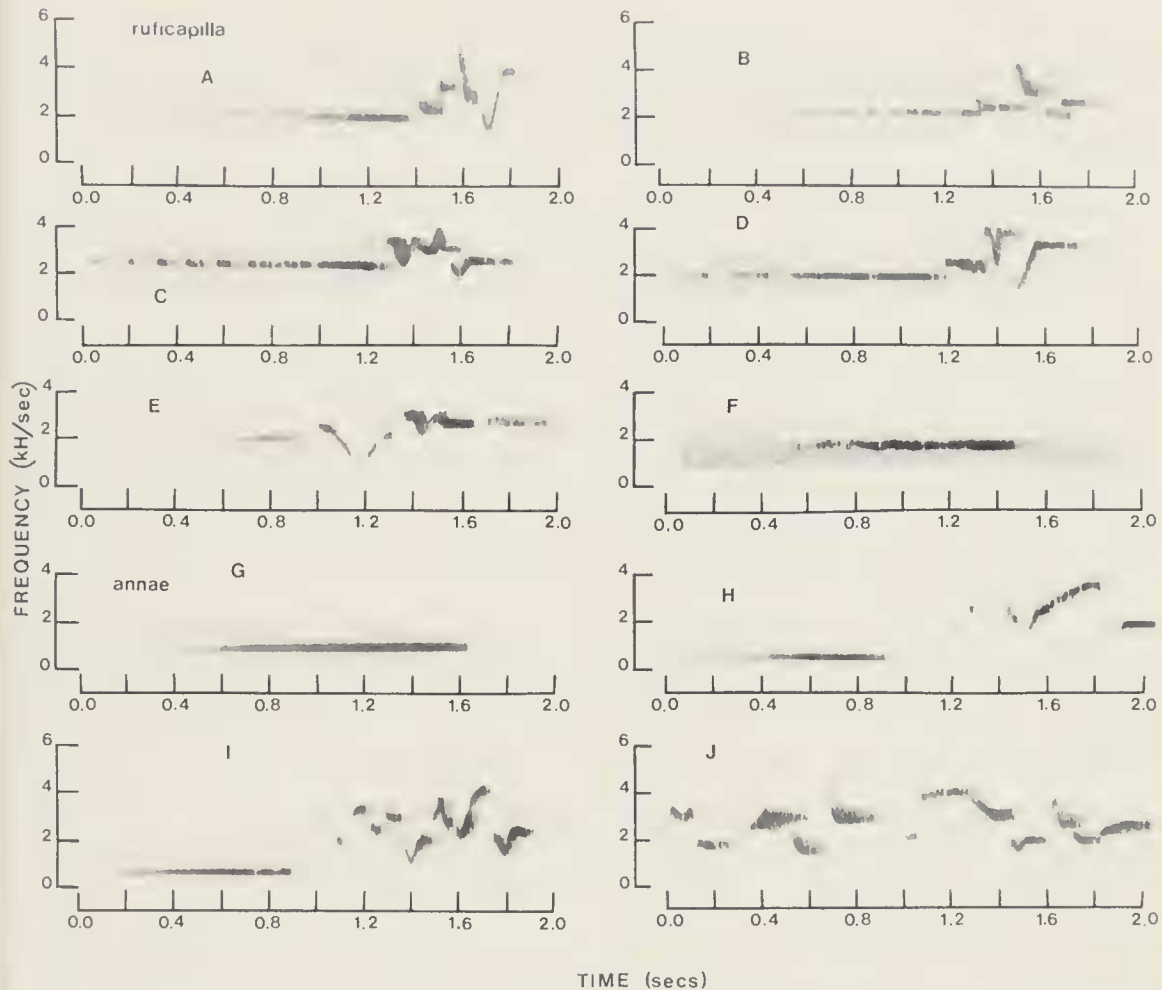


FIG. 1. Sonograms of songs of *Vitiia ruficapilla* and *Psamathia annae*. *V. r. badiceps*—A–D: four consecutive songs of a single individual, Nailagosakelo Creek, Viti Levu, Fiji, recorded 19 June 1974 (Orenstein); E–F: two songs, Savura Creek Watershed, Viti Levu, Fiji, recorded 9 July 1977 (Pratt). *P. annae*—G–I: three songs, Arakabesan, Palau, recorded 27 June 1976 (Pratt); J: “second” song, Urukthapel, Palau, recorded 2 July 1978 (Pratt). Some retouching has been necessary to clarify patterns shown here.

volume and followed by a loud warble of 2–4 phrases at a generally higher pitch. Single syllables vary considerably within a bout of singing. The whistle may be given at different pitches, and the phrases of the concluding warble may vary both in number and form. The warble may occasionally be uttered without the introductory whistle and vice versa. Figure 1 (a–f) illustrates songs of *V. r. badiceps*. Figure 1 (a–d) represents four consecutive songs of a single individual. The song of *V. r. castaneoptera* is similar in general pattern (Pratt, pers. obs.). Pairs of *V. ruficapilla* may perform duets, the song of one bird (presumably the male) being followed, or occasionally preceded, by a sharp *tsic-tsic* from the other (Watling 1982). The voice of *V. parens* is not definitely known, but Cain and Galbraith (1956:269) heard “a mellow musical whistle . . . *wuwuwi, wuwuwi* and

weedleedle wewiwi wew" on San Cristobal that was attributed by natives to this species. An unidentified song of pure whistled tones, commonly heard between 850 and 1300 m elev. on Bougainville, may be that of *V. parens* (Hadden 1981).

The primary song of *P. annae* resembles that of *V. ruficapilla* in structure, but differs in phrasing. The whistle is lower in pitch and more often given without the concluding warble (Fig. 1g). Its pitch may slur up or down, and, as in *V. ruficapilla*, may be broken by pauses near the outset. Succeeding whistles usually vary in pitch (Pratt et al. 1980). The warble, when given, may consist of more phrases than that of *V. ruficapilla*, but otherwise closely resembles the warble of the Fiji bird (Fig. 1h-i). A second song, consisting of repetitions of the warbled phrases only, resembles somewhat the "valley-crossing call" (Austin and Kuroda 1953) of *C. d. cantans* (Pratt, pers. obs.) (Fig. 1j).

The genus *Cettia* comprises three subgenera, two of which (*Cettia* and *Urosphena*) do not vocally resemble *Psamathia* and *Vitia*. Songs of Cetti's Warbler (*C. cetti*), in the monotypic subgenus *Cettia*, contain no long whistles, but are loud and uttered from concealment like those of most of the genus (Bruun and Singer 1970). The song of the Stub-tailed Bush Warbler (*C. [Urosphena] squameiceps*) is a thin, cicada-like series of notes (Dement'ev and Gladkov 1954, Yamashina 1961); that of the Bornean Short-tailed Bush Warbler (*C. [U.] whiteheadi*) a long drawn-out squeak (Smythies 1960); that of the Pale-footed Bush Warbler (*C. [U.] pallidipes*) a loud *rip . . . rip-chick-a-chick* (Fleming et al. 1976); while that of the Timor Bush Warbler (*C. [U.] subulata*) is apparently unknown.

Figure 2 illustrates the songs of four species of the third subgenus of *Cettia*, *Horeites*. Except for those of the Gray-sided Bush Warbler (*C. brunnicrons*) (Fig. 2f-g) and Müller's Bush Warbler (*C. vulcania*), these songs resemble those of *Vitia* and *Psamathia* in being divisible into two parts, the first of which is a clear, unmodulated or slowly modulated whistle or series of whistles. In the extremely drawn-out song of the Yellowish-bellied Bush Warbler (*C. acanthizoides*) the concluding portion is a trill of 10 sec or so duration. The songs of *C. diphone* and the Strong-footed or Brownish-flanked Bush Warbler (*C. fortipes*), however, conclude with a warble closely resembling that of *P. annae* or *V. ruficapilla*. The warble of *C. fortipes*, however, consists of longer, more widely spaced and broadly modulated phrases than those of *C. diphone*, *P. annae* or *V. ruficapilla*, although as the warbles of all four species are highly variable these differences may not be consistent. Figure 2e shows a song of *C. vulcania*, a species recently separated from *C. fortipes* primarily on the basis of its distinctive voice (Wells 1982).

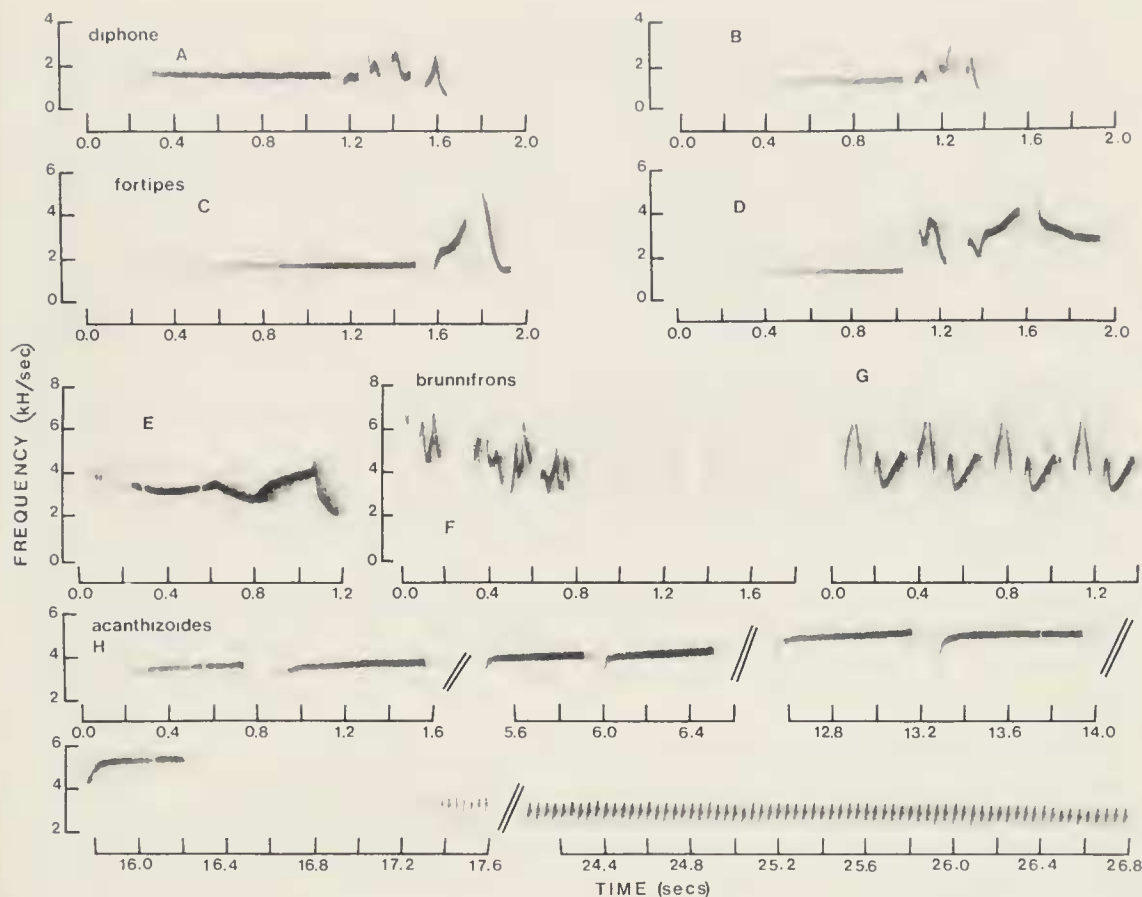


FIG. 2. Sonograms of *Cettia* (*Horeites*) spp. *C. diphone cantans*—A–B: two songs, Chichibu, Saitama Prefecture, Japan, recorded April 1961 (Japan Broadcasting Corp.). *C. fortipes davidianus*—C–D: two songs, Wu She (Nantou), Taiwan, recorded 9 August 1966 (S. R. Severinghaus). *C. vulcania oreophila*—E: song, Mount Kinabalu, Sabah, Borneo, recorded 1977 (B. King). *C. brunnifrons*—F–G: two songs, upper Arun Valley, east Nepal, recorded 23 June–3 July 1973 (E. W. Cronin, Jr.). *C. acanthizoides*—H: song (excerpts), Yuan Feng (Nantou), Taiwan, recorded 29 April 1967 (S. R. Severinghaus).

The song of the Chestnut-Crowned Bush Warbler (*C. major*) has not been described. Tapes were not available for the song of the Aberrant Bush Warbler (*C. flavolivacea*), described as “a short, very high and thin whistle” by Ali (1977:174). Among the species examined, however, *C. fortipes* and particularly *C. diphone* show the closest vocal resemblance to *Psamathia* and *Vitia*, indeed resembling these species more than they do other species of *Cettia*.

Eggs and nests.—Several clutches of eggs of *V. r. badiceps* have been collected (Nehrkorn 1879, Oates and Reid 1905). The eggs are reddish-chocolate or chocolate in color, and moderately to highly glossy (Oates and Reid 1905). These eggs are, according to Nehrkorn (1879), virtually identical to those of *P. annae*, *C. diphone*, and *C. cetti*. Pratt et al. (1980)

TABLE I
 MENSURAL CHARACTERS OF SIX FORMS OF *CETTIA*, *PSALYTHIA* AVVAE, AND FIVE FORMS OF *VITIA*

	Sex	Wing chord (mm)		Tarsus		Tail ^a		Culmen (total length)	
		$\bar{x} \pm SD$	(N)	$\bar{x} \pm SD$	(N)	$\bar{x} \pm SD$	(N)	$\bar{x} \pm SD$	(N)
<i>C. m. major</i>	m	59.9	(2)	24.3	(1)	44.1	(2)	12.1	(2)
	f	56.6	(2)	23.4	(2)	43.2	(2)	11.0	(1)
<i>C. fortipes pallidus</i>	m	54.9 ± .291	(5)	20.8 ± .066	(5)	51.7 ± .319	(5)	11.0 ± .033	(5)
	f	49.4 ± .158	(3)	19.4 ± .024	(3)	45.7 ± .074	(3)	10.6 ± .014	(3)
<i>C. f. everetti</i>	m	50.1	(2)	21.1	(2)	50.0	(2)	10.9	(2)
	f	48.7	(2)	21.0	(2)	46.6	(2)	11.0	(2)
<i>C. diphone canturians</i>	m	72.8 ± .012	(3)	27.3 ± .082	(3)	73.2 ± .247	(3)	14.3 ± .098	(3)
	f	58.6	(1)	23.5	(1)	56.7	(1)	12.4	(1)
<i>C. d. cantans</i>	m	63.6 ± .118	(9)	24.7 ± .088	(8)	64.5 ± .253	(9)	12.8 ± .087	(9)
	f	54.2	(2)	21.5	(2)	52.1	(2)	11.2	(2)
<i>C. d. seebohmi</i>	m	56.3 ± .159	(5)	24.0 ± .091	(5)	62.9 ± .238	(5)	12.3 ± .035	(5)
	f	51.4 ± .197	(4)	22.4 ± .068	(4)	57.5 ± .079	(3)	10.9 ± .076	(3)
<i>P. annae</i>	m	71.3 ± .500	(7)	29.0 ± .070	(8)	60.2 ± .526	(8)	18.2 ± .206	(5)
	f	66.6 ± .350	(6)	28.2 ± .140	(6)	56.2 ± .193	(5)	17.2 ± .160	(5)
<i>V. parens</i>	m	57.7 ± .103	(3)	25.8 ± .031	(3)	49.7		14.9 ± .025	(3)
	f	52.9	(2)	23.9	(2)	—		15.3	(2)
<i>V. r. badiceps</i>	m	54.9 ± .218	(14)	24.3 ± .116	(12)	52.1 ± .252	(10)	13.5 ± .057	(13)
	f	51.6 ± .276	(8)	23.0 ± .108	(7)	50.4 ± .224	(8)	13.4 ± .054	(8)
<i>V. r. ruficapilla</i>	m	56.8 ± .105	(9)	24.3 ± .049	(9)	56.4 ± .194	(7)	14.9 ± .085	(9)
	f	52.0 ± .153	(9)	22.7 ± .059	(9)	50.2 ± .133	(7)	14.7 ± .041	(6)
<i>V. r. funebris</i>	m	60.0 ± .180	(7)	26.6 ± .051	(8)	56.2 ± .237	(6)	14.9 ± .056	(7)
	f	56.3 ± .308	(3)	25.6 ± .101	(3)	53.4 ± .432	(3)	15.0	(2)
<i>V. r. castaneoptera</i>	m	56.6 ± .288	(9)	24.5 ± .089	(8)	57.5 ± .336	(8)	15.5 ± .088	(9)
	f	54.4 ± .142	(3)	24.0 ± .096	(3)	54.6 ± .216	(3)	14.9	(2)

TABLE 1
CONTINUED

	Sex	Culmen (from nostril) ^b		Bill width ^b		Bill depth ^b		Wing chord ratio (m/f)
		$\bar{x} \pm SD$	(N)	$\bar{x} \pm SD$	(N)	$\bar{x} \pm SD$	(N)	
<i>C. m. major</i>	m	7.1	(2)	2.5	(2)	2.5	(2)	1.06
	f	6.5	(1)	2.3	(1)	2.3	(1)	
<i>C. f. pallidus</i>	m	6.4 ± .017	(5)	2.2 ± .011	(5)	2.6 ± .009	(5)	1.11
	f	6.7 ± .028	(3)	2.4	(2)	2.6	(2)	
<i>C. f. everetti</i>	m	7.4	(2)	2.9	(2)	2.7	(2)	1.03
	f	7.5	(2)	3.0	(2)	2.6	(2)	
<i>C. d. canturians</i>	m	8.9 ± .065	(3)	3.7 ± .026	(3)	4.4	(1)	1.24
	f	7.5	(1)	2.8	(1)	3.7	(1)	
<i>C. d. cantans</i>	m	8.1 ± .043	(9)	3.1 ± .025	(9)	3.3 ± .017	(8)	1.17
	f	7.3	(2)	2.5	(2)	2.7	(2)	
<i>C. d. seebohmi</i>	m	8.0 ± .018	(5)	3.2 ± .007	(5)	3.2 ± .016	(5)	1.10
	f	7.9 ± .021	(3)	2.8 ± .005	(3)	3.0 ± .026	(3)	
<i>P. annae</i>	m	12.2 ± .090	(5)	3.7 ± .023	(7)	3.4 ± .014	(6)	1.07
	f	11.4 ± .072	(5)	3.4 ± .022	(6)	3.2 ± .005	(5)	
<i>V. parens</i>	m	10.2 ± .006	(3)	3.3 ± .006	(3)	3.3 ± .021	(3)	1.09
	f	10.3	(2)	3.3	(2)	3.2	(1)	
<i>V. r. badiceps</i>	m	9.3 ± .040	(13)	3.0 ± .005	(9)	3.0 ± .218	(4)	1.06
	f	9.1 ± .068	(7)	2.8 ± .005	(7)	2.8	(2)	
<i>V. r. ruficapilla</i>	m	10.1 ± .049	(9)	3.2 ± .013	(8)	3.0 ± .013	(5)	1.09
	f	9.9 ± .030	(7)	3.1 ± .016	(7)	2.9 ± .013	(3)	
<i>V. r. funebris</i>	m	10.1 ± .043	(7)	3.3 ± .009	(7)	3.5	(2)	1.07
	f	9.8	(2)	3.2	(2)	—		
<i>V. r. castaneoptera</i>	m	10.2 ± .034	(9)	3.2 ± .014	(9)	3.1 ± .015	(3)	1.04
	f	10.5	(2)	3.4	(2)	3.1	(1)	

^a Tails exhibiting marked wear were not measured.^b Measurements of culmen (from nostril), bill width, and bill depth were taken at the level of the anterior end of the nasal cavity. (Bill depth was not measured on specimens with improperly occluded bills.)

also describe a dark purplish-brown egg of *P. annae*. Such dark egg colors are unusual among passerines, and egg color has been used as a generic character in *Cettia* (Mayr, in litt.).

Vitia ruficapilla builds a "large, rather crude nest . . . domed with the entrance hole above mid-height, on one side" (Watling 1982:108). Nest structure is variable in *Cettia*. *C. f. fortipes* builds nests "varying from a deep cup to a domed or globular structure with a large entrance near the top" (Ali and Ripley 1973:11). Pratt et al. (1980) commented on the similarity of the nest of *P. annae* to the domed nest of *C. d. cantans* described by Austin and Kuroda (1953). The nest of *C. d. borealis* is a deep, symmetrical cup (Dement'ev and Gladkov 1954).

Morphology.—*Vitia* and *Psamathia* resemble species of *Cettia*, particularly those in the subgenus *Horeites*, in size, proportions, and plumage pattern (Tables 1, 2; Fig. 3; cf. Delacour [1942–43] for analyses of subgenera). They differ chiefly in having longer bills, a feature common in insular representatives of mainland genera (Grant 1965, Schoener 1965). Within *Cettia*, insular races of *C. diphone* (*diphone*, *restrictus*) have longer bills than the continental (*borealis*, *sakhalinensis*, *canturians*) or main-land Japanese (*cantans*) subspecies (Vaurie 1954, 1959). *Cettia*, *Vitia*, and *Psamathia* all differ from most sylvine genera in having 10, rather than 12, rectrices (Ali and Ripley 1973; Orenstein, pers. obs.). This distinction also sets these warblers apart from *Sericornis* (Acanthizinae) to which *V. parens* has been compared (Mayr 1936). The rufous to chestnut crown and cinnamon face of *V. parens* and *V. ruficapilla* resemble those of *C. major*, *C. brunnifrons*, and particularly *C. d. seebohmi*.

Among themselves, the two species of *Vitia* and *P. annae* exhibit few divergences. *Vitia parens* differs from *V. ruficapilla* primarily in being browner, with a more extensive cinnamon wash on the cheeks. Means for the three males measured fall within the range of means for races of *V. ruficapilla* for all characters examined except tail length, for which wear may have affected the results (Tables 1, 2). *Psamathia annae* differs from both *Vitia* spp. in lacking rufous or cinnamon in the plumage and in larger size. In these respects the Palau Bush-Warbler closely resembles *C. d. cantans* of Japan.

The juvenile of *V. parens*, known from a unique specimen in the American Museum of Natural History (Mayr 1936), differs markedly from its adult but resembles fairly closely the adult plumage of *P. annae* (Table 2, Fig. 2). It shares with *P. annae*, though not with the adult *V. parens*, a generally olive coloration with a bright olive-yellow throat. Although it differs from the Palau bird in being darker with a blackish crown and brown thighs and flanks, and in lacking a superciliary stripe, placed between specimens of *V. parens* and *P. annae* it might easily be taken for the young of the latter rather than of the former.

TABLE 2
 PLUMAGE CHARACTERISTICS OF *CETTIA DIPHONE*, *PSAMATHIA ANNAE*, *VITIA PARENS* AND *V. RUFICAPILLA*

	Crown	Back	Face and cheeks	Underparts
<i>C. d. cantans</i>	Olive Green ^a	Olive Green	Olive Grey	Pale Grey washed with Citrine
<i>C. d. seebohmi</i>	Cinnamon Brown (brighter than back)	Cinnamon Brown	Medium Neutral Grey, washed with Cinnamon	Grey, washed with Olive on flanks
<i>P. annae</i>	Greyish Olive	Greyish Olive	Olive Yellow, brightest on throat	Olive Yellow
<i>V. parens</i> (juv.)	blackish	dark Greyish Olive	Olive Yellow; center of throat bright Olive Yellow	Olive Yellow; thighs and flanks brown
<i>V. parens</i> (ad.)	Russet	Olive Brown (darker than <i>ruficapilla</i>)	Cinnamon (extends to throat)	Olive washed with Cinnamon
<i>V. r. ruficapilla</i>	Cinnamon Rufous	Olive Brown	Cinnamon	Grey washed with Olive on flanks
<i>V. r. badiceps</i>	Chestnut	Olive Brown	Medium Neutral Grey, washed with Cinnamon	Grey washed with Olive on belly and flanks
<i>V. r. funebris</i>	Russet	Olive Brown (darkest and greyest race)	Cinnamon, mottled with blackish	Grey, washed with Olive on belly and flanks
<i>V. r. castaneoptera</i>	Chestnut	Olive Brown (brownest race)	Medium Neutral Grey, washed with Cinnamon	Grey, washed with Olive on flanks

^a Capitalized names of colors from Smithe (1975).



FIG. 3. Specimens of male *Cettia diphone*, *Vitia* spp. and *Psamathia annae* photographed at the American Museum of Natural History, New York. From left: *Cettia diphone cantans* (AMNH 596788), *C. d. seebohmi* (AMNH 416882), *Vitia ruficapilla castaneoptera* (AMNH 251977), *V. r. funebris* (AMNH 251965), *V. r. ruficapilla* (AMNH 251956), *V. r. badiceps* (AMNH 251997), *V. parens* (ad.) (AMNH 228061), *V. parens* (juv.) (AMNH 228062), *Psamathia annae* (AMNH 332079).

GENERIC LIMITS

The presence of pure monotonal whistles as song components might be the result of similar selection pressures. The Fiji Warbler, the Shade Warbler, the Palau Bush-Warbler, as well as many bush-warblers of the genus *Cettia*, are all birds of the lower forest levels. Pure whistles may have selective value related to their carrying ability in the forest understory (Morton 1975), and occur in the songs of understory species of many diverse avian families. Similar whistles occur, for example, in the African sylvine genus *Bathmocercus* (Chappuis 1980). But the whistle-warble songs of *P. annae*, *V. ruficapilla*, *C. fortipes*, and *C. diphone* appear too similar to be the result of simple habitat similarities. All *Horeites* spp., including those whose songs are not like those of *Psamathia* and *Vitia*, are birds of forest understory (Ali and Ripley 1973, King et al. 1975).

Some doubt the utility of egg color in taxonomy (Lack 1958). The unusually dark egg colors of *Psamathia*, *Vitia*, and *Cettia* (*Horeites*), how-

ever, probably represent a synapomorphy (i.e., a shared derived character).

Rectrix number is not always a valid generic character. The Cinnamon Bracken Warbler (*Bradypterus cinnamomeus*), an African sylvine placed in a genus allied with *Cettia*, may have either 10 or 12 rectrices (Delacour 1942–43). The presence of 10 rectrices, however, as with dark egg color, is sufficiently rare in the Sylviinae to be of significance when it occurs in species that share other apparently derived characters. And while the general similarities of plumage and body proportions cannot carry much taxonomic weight in a group containing as many similar species as do the Sylviinae, they reinforce the conclusion that *Vitia*, *Psamathia*, and *Cettia* are closely related.

On the basis of song structure, egg color, and external morphology, therefore, we believe that *Vitia* and *Psamathia* are best regarded as sharing a common ancestry with *C. diphone* within *Horeites*, and thus underserving of generic or even subgeneric status. Following this proposal the species *C. annae*, *C. parens*, and *C. ruficapilla*, here listed alphabetically and in order of increasing distance from continental Asia, should be included in the subgenus *Horeites* following *C. diphone*. The genera *Vitia* (with its synonym *Drymochaera*) and *Psamathia* should be added to the synonymy of *Cettia*. *Gladkovia* (Kashin 1977), proposed as a replacement for *Psamathia* which the author believed to be preoccupied by a lepidopteran genus, also becomes a synonym of *Cettia*.

DERIVATION OF SOUTHWEST PACIFIC *CETTIA*

Cettia parens and *C. ruficapilla* closely resemble *C. d. seebohmi* of Luzon, while *C. annae* is more similar to *C. d. cantans* of Japan. Palearctic races of *C. diphone*, however, including *cantans*, exhibit strong sexual dimorphism in wing length, a character lacking in tropical Asian *Cettia* including *C. d. seebohmi*. The three Pacific island species exhibit little dimorphism (Table 1; Ali and Ripley 1973, Delacour 1942–43). While sexual size dimorphism may not always increase under island conditions (Selander 1966, Cruz 1977), it is unlikely to decrease. Thus, we believe the island *Cettia* were derived from a tropical, rather than a migratory temperate ancestor. Baker (1951) considered *C. d. seebohmi* a likely ancestor of *C. annae*. We prefer to view *C. d. seebohmi* as bearing a close resemblance to the ancestor of the entire *diphone-annae-parens-ruficapilla* complex. But because *C. d. seebohmi* is a montane endemic confined to Luzon, and thus an unlikely source of a Pacific radiation, we do not share Baker's (1951) conviction that *C. annae* reached Palau directly from the Philippines. Particularly since *C. parens* and *C. ruficapilla* more closely resemble *C. d.*

TABLE 3

PERCENTAGE DIVERGENCE OF MORPHOLOGICAL FEATURES IN *CETTIA ANNAE*, *C. PARENS* AND *C. RUFICAPILLA* FROM *C. DIPHONE SEEBOHMI* (MALES ONLY) BASED ON DATA IN TABLE 1

	Wing	Tarsus/ wing	Tail/ wing	Culmen/ wing	Bill width/ wing	Bill depth/ wing
<i>C. annae</i>	+26.6 ^a	(-4.5)	-24.4	+20.4	-8.8	-15.8
<i>C. parens</i>	(+2.5)	(+4.9)	-22.9	+24.6	(+1.8)	(0.0)
<i>C. r. badiceps</i>	(-2.5)	(+3.9)	-15.0	+19.0	(-3.5)	(-3.5)
<i>C. r. ruficapilla</i>	(+0.9)	(+0.5)	-11.0	+25.4	(-1.8)	-7.0
<i>C. r. funebris</i>	+6.6	(+3.9)	-16.1	+18.3	(-3.5)	(+1.8)
<i>C. r. castaneoptera</i>	(+0.5)	(+1.6)	-8.7	+26.8	(0.0)	(-3.5)

^a Values are the differences between the means for each form and *seebohmi*, expressed as a percentage of the mean for *seebohmi*; a positive value indicates a higher figure for the insular forms, a negative value a lower figure; differences of less than $\pm 5\%$ are enclosed in parentheses; presentation modified from Grant (1965).

seebohmi than does *C. annae*, we believe the latter more likely colonized Palau from the Papua-Solomons area as did several other species (Mayr 1945, Baker 1951, Ford 1979). Thus, the three Pacific island species can be viewed as relicts of a species of *Cettia*, allied to *C. diphone*, once widespread in the Indo-Pacific region.

EVOLUTION OF CETTIA IN THE SOUTHWEST PACIFIC

Table 3 presents morphological divergences from *Cettia d. seebohmi* in males of *C. annae*, *C. parens*, and *C. ruficapilla*. The Pacific species show an 18.3–25.4% increase in relative culmen length and an 8.7–24.4% decrease in relative tail length. No other consistent patterns of change are apparent (contra Baker 1951 in the case of tarsal length), although *C. annae* shows a 26.6% increase in absolute wing length and a decrease in relative bill width and depth. Even though *C. d. seebohmi* is not likely the direct ancestor of the Pacific island birds, it probably resembles that ancestor closely enough for differences between it and the insular species to approximate actual evolutionary changes.

Murphy (1938) and Grant (1965) documented increases in bill and tarsus length for insular populations of North American passerines, but noted that these do not always occur together. Grant (1965) postulated that an increase in culmen length was related to the exploitation of a wider range of food items, facilitated by ecological release in a less diverse avifauna. The increased overall size of *C. annae* may be similarly explained, although it is difficult to see why only this species has so evolved. An explanation for the decrease in tail length is even more obscure. The 24.4% reduction in tail length in *C. annae* may be related to a retention of juvenal

plumage features suggested by its resemblance to the young of *C. parens*. Wear, complicated by small sample sizes, may have biased some of the results, particularly in *C. parens* (N = 2).

We lack the ecological data required to determine whether relationships exist between morphological differences among the three island species and environmental differences among Palau, San Cristobal, and Fiji. The Fiji Warbler, geographically the species most remote from Asia, has diverged least in plumage from the ancestral pattern. A combination of *C. r. badiceps* and *C. r. castaneoptera* might produce a bird differing from *C. d. seebohmi* only in its longer bill, shorter tail, and slightly duller upperparts. While the larger size of the Palau Bush-Warbler relative to other *Cettia* might be related to the small size of the islands it inhabits, no such island association can be shown among the various subspecies of the Fiji Warbler that occur on islands ranging in size from Viti Levu (10,388 km²) to Kadavu (409 km²).

Unlike *Acrocephalus*, the only other sylvine genus widespread on Pacific islands, *Cettia* appears to have made few adaptive shifts in response to the island environment, probably because no such shifts were necessary. The success of *C. diphone* on Oahu (Berger 1972, Shallenberger 1978) attests to the adaptability of temperate *Cettia* to insular tropical forest communities. In contrast, the reedy and grassy habitats preferred by many continental *Acrocephalus* are scarce on Pacific islands, necessitating a broadening of niche for survival. Noteworthy here is that both the Nightingale Reed Warbler (*Acrocephalus luscinia*) on Saipan (Pratt et al. 1979) and the Carolines Reed Warbler (*A. syrinx*) in the Caroline Islands (Pratt, pers. obs.) occur in forests but are more abundant in thickets and grassy habitats. Holyoak and Thibault (1977) have suggested that *Acrocephalus* has been unable to colonize most of eastern Melanesia because it has been excluded by resident forest-adapted species. *Cettia*, already a forest genus, presumably possessed the necessary preadaptations to establish itself on these islands. Thus, the lack of major habitat shifts in insular *Cettia* should not necessarily be interpreted as indicating a more recent island colonization by that genus than by *Acrocephalus*. In fact, the disjunct distributions of both genera in the Indo-Pacific may indicate a very long period of residence by both.

Gaps in the present distribution of *Cettia* in the southwest Pacific cannot be entirely explained by accidents of dispersal or unsuitability of habitat on the unoccupied islands. In particular, ancestors of *C. ruficapilla* surely reached at least some of the islands between San Cristobal and Fiji, such as the New Hebrides or New Caledonia. Either they failed to establish themselves on these islands, or did so, but subsequently became extinct. The likeliest explanation for their present absence is exclusion by other

species. The Yellow-sided Warbler (*Gerygone flavolateralis*; Acanthizinae) is common on New Caledonia where it is a bird of forest undergrowth (Delacour 1966; Orenstein, pers. obs.). It is also found in the Loyalty Islands and some of the New Hebrides. Its distribution in the New Hebrides has apparently undergone changes resulting from local extinction and recolonization (e.g., on Santo) in historic times (Diamond and Marshall 1977b). It may therefore have excluded *Cettia* on islands where it, too, is absent today. On the Santa Cruz Islands, Sanford's White-eye (*Woodfordia lacertosa*) may have excluded *Cettia*. The apparent restriction of *C. parens* within the Solomons to the highlands of San Cristobal, and, probably, Bougainville, may be the result of diffuse competition (Diamond and Marshall 1977a). Perhaps *C. r. funebris* is being excluded from the lowlands of Taveuni by the Silktail (*Lamprolia victoriae*), also an insectivorous understory species. On Viti Levu, where *Lamprolia* is absent, *C. r. badiceps* occurs commonly down to sea level (Holyoak 1979; Orenstein, pers. obs.). The present distribution of *Cettia* in the southwest Pacific resembles that of a population in Stage III of a taxon cycle (Ricklefs and Cox 1972, 1978).

Assigning *Vitia* and *Psamathia* to the synonymy of *Cettia* makes this the only southwest Pacific land bird genus definitely derived from Asia but absent from either New Guinea or Australia. Along with *Hirundo*, *Acrocephalus*, *Zoothera*, and *Turdus*, it forms one of the few northern elements in an otherwise Australasian avifauna. Whether it is a recent arrival in the area or has been present for a long time, its distribution is of considerable biogeographical, as well as taxonomic, importance.

SUMMARY

The sylviine genera *Vitia*, with different species on San Cristobal and Fiji, and *Psamathia*, a monotypic genus endemic to Palau, are here assigned to the subgenus *Horeites* of the genus *Cettia* on the basis of similarities in voice, egg color, and morphology. Within *Cettia*, the species *C. annae*, *C. parens*, and *C. ruficapilla* may share common ancestry with *C. diphone*. Their continental ancestor probably resembled *C. diphone seebohni* of Luzon, but a direct Philippine derivation of these forms is unlikely. A colonization route through Indonesia, with *C. annae* reaching Palau from the Papuan region, is proposed. The three species may be relicts of a single formerly widespread Indo-Pacific species. The insular species have evolved longer bills and shorter tails than *C. d. seebohni*. *Cettia annae* has become significantly larger, and its plumage may represent a retention of juvenile characteristics as shown by the young of *C. parens*. The Pacific species of *Cettia* have undergone few shifts in habitat choice. Competitive exclusion may be responsible for the absence of *Cettia* from suitable islands between San Cristobal and Fiji. The expanded genus *Cettia* is the only southwest Pacific land bird genus of Asian origin that is absent from New Guinea or Australia.

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